A new Lower Ordovician bivalve family, the Thoraliidae (? Nuculoida), interpreted as actinodont deposit feeders

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Synopsis

A new bivalve family, based on the Lower Ordovician *Thoralia languedociana* (Thoral) gen. nov., is described. It has a shell shape and musculature typical of the Nuculoida but subumbonal cardinal hinge teeth.

Introduction

Material from the early Ordovician (Lower Arenig) of the Montagne Noire of southern France collected by Professor W. T. Dean includes a well-preserved specimen of '*Leda*' *languedociana* Thoral 1935 in which many of the details of the hinge and muscle attachment are preserved.

The species has a shell form typical of mobile protobranch nuculoids but lacks their taxodont teeth. In fact it has a hinge structure having more features in common with the actinodonts than with the nuculoids. This morphology has led me to erect a new genus, *Thoralia*, and family Thoraliidae, for the species. It is tentatively placed in the order Nuculoida, but the family does not fit with any certainty in any of the existing three superfamilies of the Nuculoida. It is among the earliest nuculoid species described where any details of the hinge and muscle attachment are known.

Thoralia languedociana occurs in argillaceous quartz silt sediment where infaunal bivalves form an important part of the fauna. They are associated with bellerophonts, rostroconchs, cephalopods, hyoliths, brachiopods and many trilobites (Thoral 1935 : 329). The fauna is of a more varied nature than those so far described in more inshore facies of the Lower Arenig, especially sands where bivalves predominate. This is true both when the bivalves alone and also when all the Mollusca are considered (Morris 1978 : fig. 25). The nature of the sediment and its fauna suggests an offshore shelf environment.

Orientation

At least three independent characters indicate the correct orientation of *Thoralia*. First, the subrostrate margin, which is interpreted as posterior. Secondly, there is only one possible position in which the ligament could have been situated; this is interpreted as posterior to the umbones. Thirdly, the form and position of the pedal/body attachment muscle scars are closely similar to those in a number of known nuculoids where the orientation is not in doubt.

Nuculoid affinities of *Thoralia*

The shape, ornament and musculature suggest that *Thoralia* is a nuculoid. The shape is very similar to that of a number of genera of Recent Nuculanacea, and it also has some less exact but broad similarities to other Palaeozoic nuculoids, including *Ctenodonta*, *Tancrediopsis* and *Praectenodonta* of the Ctenodontacea and *Palaeoneilo*, *Paleyoldia* and *Phestia* of the Nuculanacea. The only other bivalves that have a remotely similar shape occur within the Tellinacea, the Corbulidae which are in nearly every case more gibbous, and the little known Myophoricardiidae. All of these occur in Mesozoic or younger rocks and I consider them to be offshoots of late Palaeozoic Crassatellacea or just possibly, in the case of the corbulids, the Anomalodesmata.

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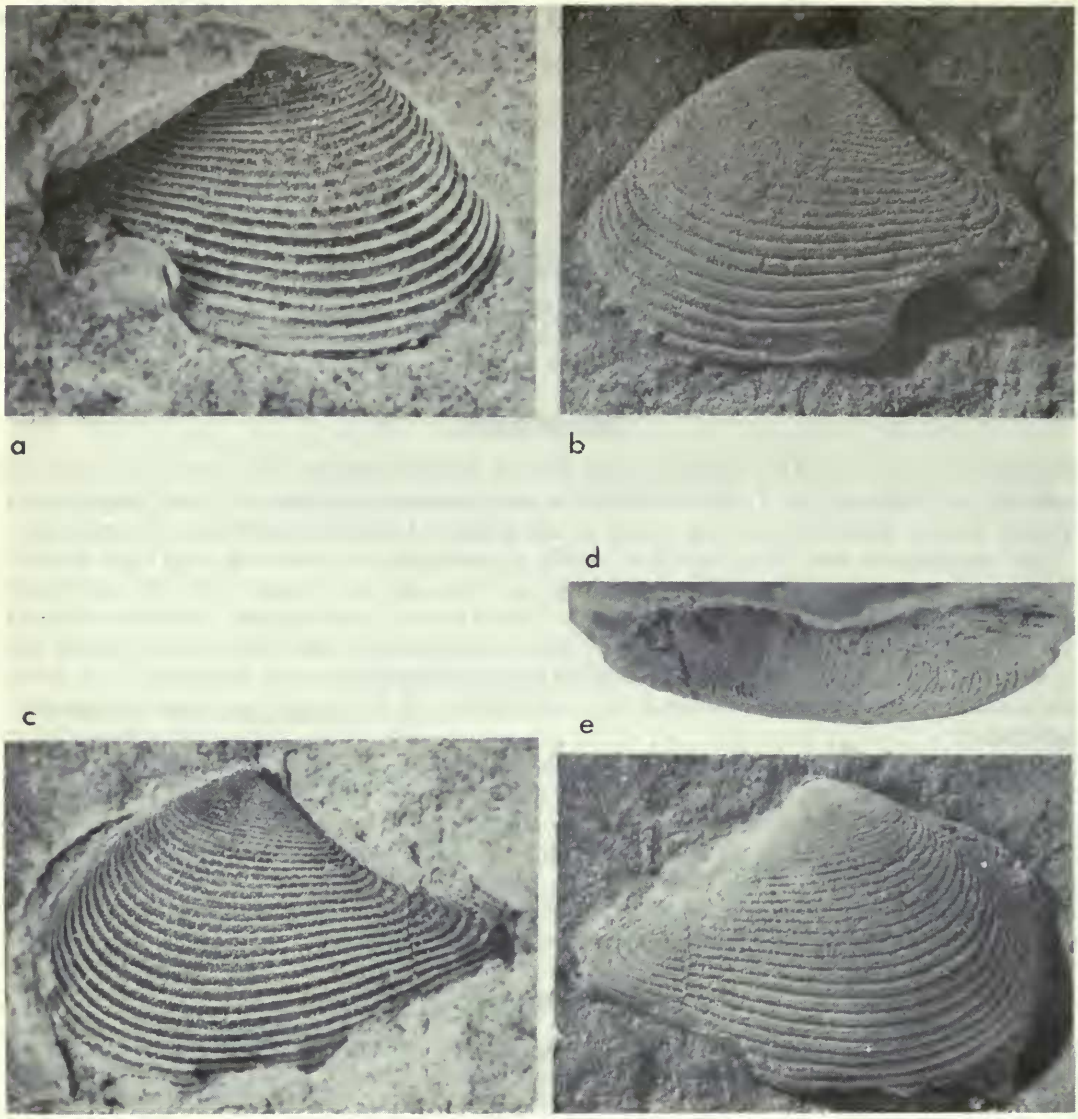

Fig. 1a–e *Thoralia languedociana* (Thoral), L. Arenig, Félines, southern France, all *c.* ×8. a, natural external mould of left valve. b, left valve, latex rubber cast. c, natural external mould of right valve. d–e, right valve, latex rubber cast; d, dorsal view, e, lateral view.

The Tellinacea include secondarily developed deposit feeders whose shape may also be related to their efficient motion through soft sediment.

The elongate shape of *Thoralia* is indicative of good burrowing ability but the relatively thick shell suggests that it did not move rapidly (Stanley 1970).

The enlarged illustrations of the shell suggest that it is more coarsely sculptured than is usual for nuculoids, but this is an illusion owing to the small size; *Thoralia* is only 7·8 mm long. The close spacing of the comarginal ribs is of common occurrence in many genera of nuculoids. No pallial line is preserved in *Thoralia* but it is considered unlikely that either a pallial sinus or extensive siphons were present. A pallial sinus is not known in any other Lower or Middle Ordovician nuculoid and it has not been considered that the one possibly sinupalliate Ordovician

Fig. 2 *Thoralia languedociana* (Thoral), steinkern viewed from left side, *c.* ×8.

genus, *Lyrodesma* (Lyrodesmatidae), had particularly extensive siphons. Even in sediments through which oxygenated ground-water may be freely circulating, non-siphonate bivalves such as the Glycymerididae and possibly some Crassatellacea are not known to be deep burrowers. It is therefore very probable that *Thoralia* was also a shallow burrower. The ribbing of the posterior part of the shell is at its most prominent at the rounded carina separating the dorsal area from the shell side and may have served to prevent scouring (Stanley 1977).

Although the specimen of *Thoralia* is very small, seven pairs of pedal/body attachment muscle scars are clearly preserved (Figs 2, 3, 7). They are slightly uneven in their depth of insertion and their disposition along a curving line between the adductor scars. The anterior and posterior pedal retractors (nos 1 & 7) are the most deeply inserted. The two pairs (nos 2 & 3) lying anterior to the umbones occur lower on the flank than the more posterior pairs (nos 4, 5 & 6). Pairs nos 1–4 form a convexly-downward curve on either side, which closely resembles the attachment scars of the wall of muscular tissue surrounding a body cavity in living nuculoids (Heath 1937) and visible in many fossil species (Bradshaw 1978).

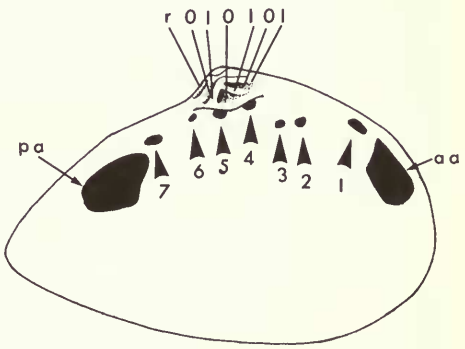

Fig. 3 *Thoralia languedociana* (Thoral), reconstruction of left valve, internal view, ×11. I–hinge teeth, O–sockets, r–ligament groove, 1–7 –pedal/body attachment muscle scars, aa–anterior adductor muscle scar, pa–posterior adductor muscle scar.

Evolutionary interpretation of *Thoralia*

Because of the rounded blade-like anterior (*sensu* Stanley 1970) of *Thoralia* and its general similarity in shell shape to living nuculoids, I interpreted this genus as a mobile infaunal deposit feeder (Morris 1979). I also suggested that the inferred existence of early non-taxodont deposit feeders offers some support for the view that deposit feeding may have been a more primitive mechanism than filter feeding within the Bivalvia as a whole (Morris 1979). A plausible model for the evolutionary development of bivalve filter feeding is outlined in Fig. 4.

The existence of this early bivalve with characters of the Nuculoida, except for the number

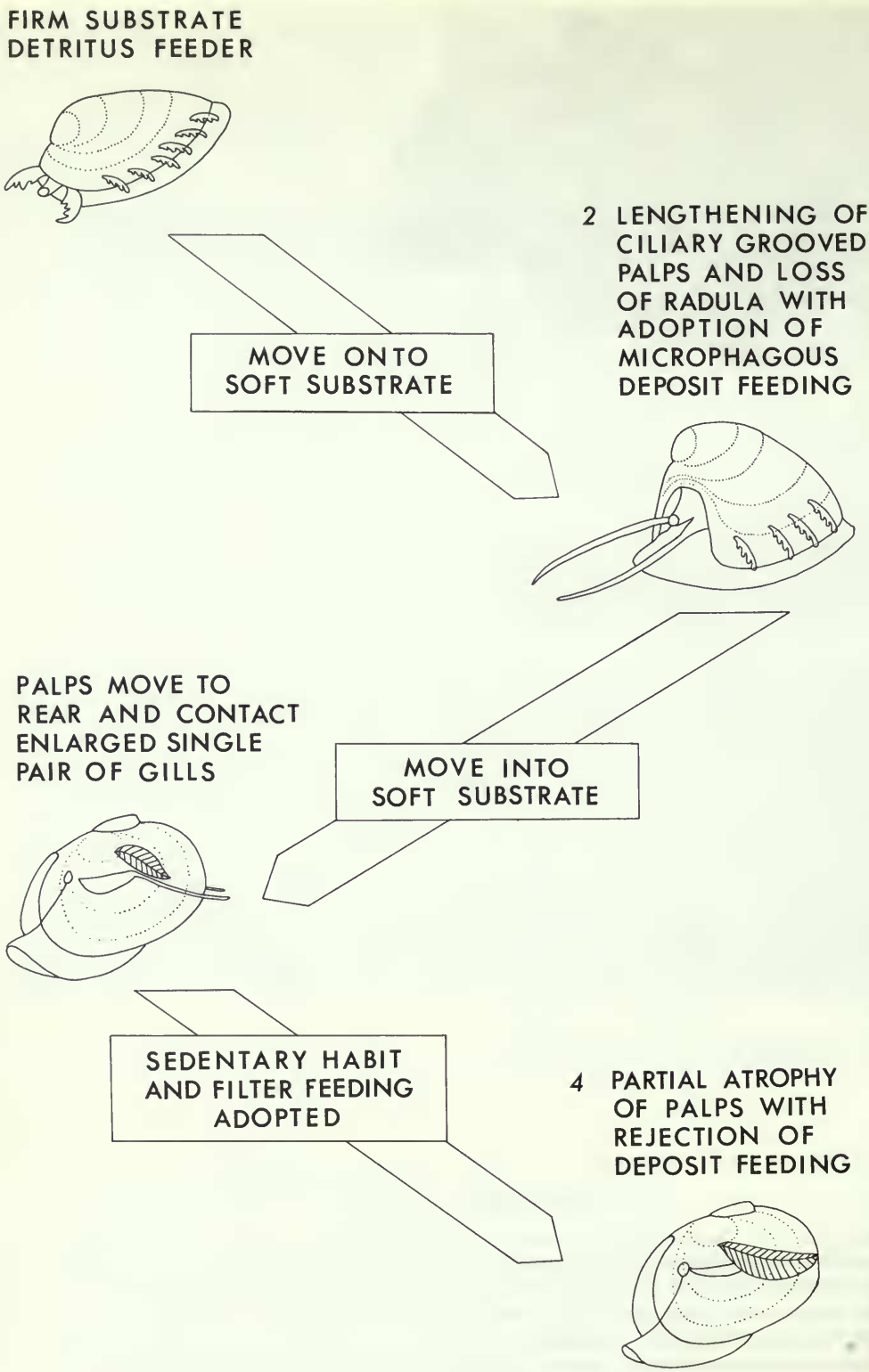

Fig. 4 A hypothetical model for the origin of bivalve filter feeding.

and disposition of the hinge teeth, is consistent with the view that a small, rather than a large, number of hinge teeth is the more primitive condition for the Bivalvia. Other evidence for this includes the distribution in other Lower Ordovician bivalves of hinge teeth types which I previously summarized (Morris 1979), and also the ontogenetic development of the Ordovician nuculoid *Tironucula* (Morris & Fortey 1976, Morris 1979). In addition, in one of the earliest known bivalves, the Lower Cambrian *Fordilla sibirica* Krasilova, the dentition has recently been described (Krasilova 1977, Pojeta 1978). This consists of single interlocking teeth and sockets occurring in front of the umbones, an arrangement comparable to the first-formed teeth of *Tironucula*.

A possible outline of the relationships of *Thoralia* based on these views is shown diagrammatically in Fig. 5.

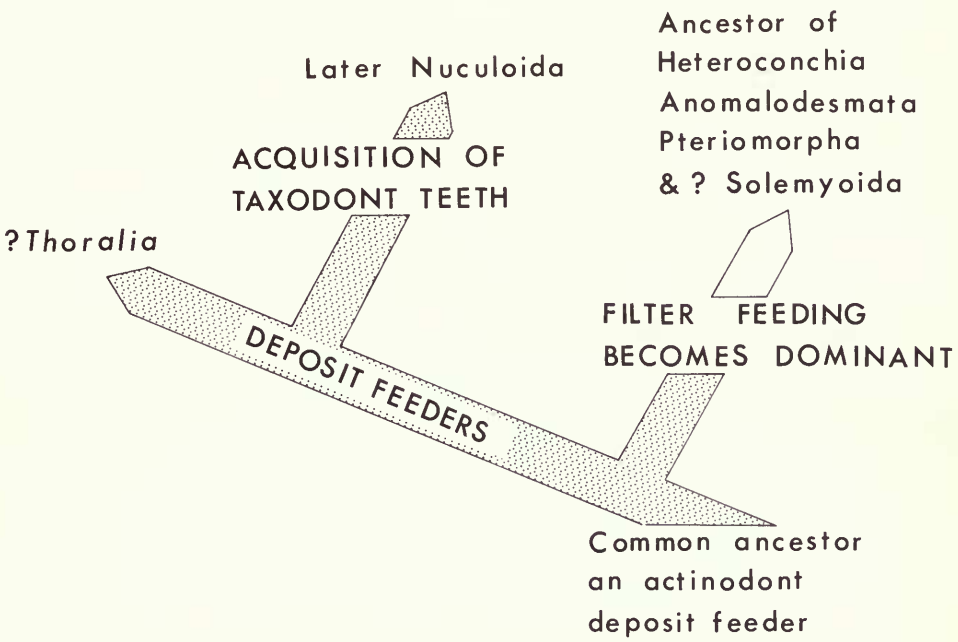

Fig. 5 Suggested relationships of *Thoralia*.

Systematic description

Class **BIVALVIA** Linnaeus, 1758

? Subclass **PALAEOTAXODONTA** Korobkov, 1954

? Order **NUCULOIDA** Dall, 1889

Superfamily uncertain

Family **THORALIIDAE** nov.

FAMILY DIAGNOSIS. Small bivalves of nuculoid shape with four radiating subumbonal cardinal teeth.

REMARKS. This combination of shape and hinge structure distinguishes the Thoraliidae from all other bivalve families.

TYPE and only genus *Thoralia* gen. nov.

Genus *THORALIA* nov.

DIAGNOSIS. As for family.

TYPE SPECIES. *Leda languedociana* Thoral 1935; no other species are known.

DESCRIPTION. As for species.

Thoralia languedociana (Thoral 1935)
Figs 1, 2, 6, 7

1935 *Leda languedociana* Thoral : 164–165; pl. 13, figs 2–3.

TYPES. A syntypic series described by Thoral (1935) consisting of four specimens in a fine siltstone nodule from the Bois de la Cabosse, north of Assignan (J. Miquel coll. no. 475), and one specimen from a nodule from the Lower Arenig at St Chinian (Villebrun coll.). Thoral thought that all these specimens came from his 'horizon à *Miquelinia miqueli*', which he considered to belong to the Lower Arenig. The specimens are in the collections of the Laboratoire de Paléontologie des Invertébrés, Academie de Montpellier, France.

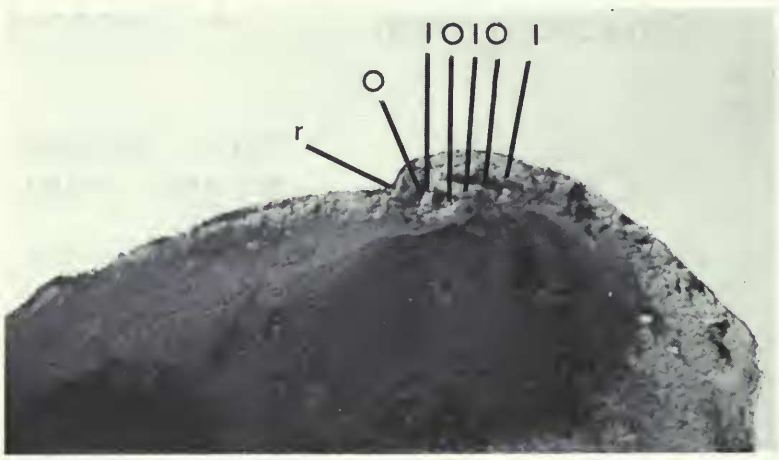

Fig. 6 *Thoralia languedociana* (Thoral). Latex rubber mould of the hinge of the left valve, ×16. I–hinge teeth, O–sockets, r–ligament groove.

OTHER MATERIAL. A single specimen with the internal and external mould of both valves in Palaeontology Dept., British Museum (Natural History) (LL 31371), L. Arenig, Vigne, below and west of Rocs de Fayrols, near Camploug, Félines, France (W. T. Dean coll.).

DESCRIPTION. The latter specimen is small and tear-shaped or nuculaniform. The anterior is rounded and the posterior subrostrate. The anterodorsal and ventral margins are subparallel. The umbones are central and opisthogyrate. The posterodorsal area is separated from the flank by a distinct change of angle which forms a rounded edge from the umbones to the posteroventral margins. There is no lunule nor escutcheon.

The sculpture consists of closely packed strong co-marginal rounded ribs separated by narrow slit-like interstices.

There are short, strong hinge plates below the umbones with three small radiating teeth in the left valve (Figs 3, 6). The anterior tooth may be confluent with the dorsal margin. There are four interlocking teeth on the hinge plate of the right valve which is less well preserved. On the articulating surface between the anteriormost tooth of the right valve and the tooth behind it in the left valve there are at least four interlocking denticles, which appear as four oblique striations similar to those of many Cycloconchacea, Trigonidae and Unionidae.

The point of attachment of the ligament is not altogether clear. There is no distinct nymph, but the only position where the ligament could fit is in a very restricted region on the unfortunately obscured dorsal edge of the posterodorsal margin, immediately below and behind the umbones.

The muscle scars (Figs 2, 3, 7) consist of nearly isomyarian adductors, in which no separation into quick and catch is evident, and a series of six pairs of pedal/body attachments which lie between the adductors high on the internal shell surface.

The anterior adductor is moderate-sized, elongate oval, situated close to the anterior margin above its mid-point. The posterior adductor is situated on the posterodorsal area with a rounded posterior and ventral margin. Its dorsal margin runs parallel and close to the dorsal shell margin and it is truncated anteriorly. Because of its position so high in the shell, the scar is set at a considerable angle to the plane of commissure, so that the lower part of the adductor muscle joining the two valves would have been much longer than the upper part.

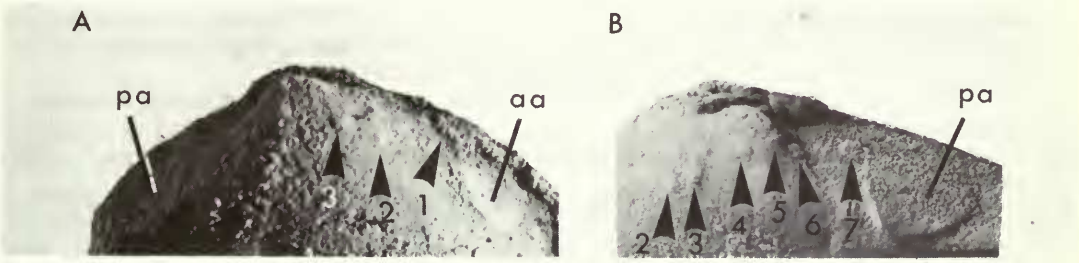

Fig. 7 Muscle attachment scars of *Thoralia languedociana* (Thoral), *c.* ×8; steinkern showing pedal and adductor muscle attachment scars. A, dorsal portion of interior of right valve. B, part of dorsal portion of interior of left valve, oblique view. aa–anterior adductor, pa–posterior adductor, 1–7 – pedal/body attachment muscles.

The anterior pedal retractor (1, Fig. 7) is small, deep-set and rounded and is situated close to the anterior dorsal margin on the umbonal side of the anterior adductor. Pedal scars 2 and 3 are apparently elongate in a dorsoventral direction. Their traces are difficult to separate but this may only be because of imperfect preservation, and their length therefore may be less than appears. They are situated relatively low on the shell side below the anterior part of the hinge plate. Pedal muscle scars 4, 5 and 6 lie close under the umbones. The posterior pedal retractor, 7, lies close to the dorsal shell margin on the umbonal side of the posterior adductor.

Dimensions. Right valve of LL 31371: length 7·8 mm, height 5·48 mm, width 1·66 mm.

Discussion. The elongate teardrop-like shape of this species led Thoral to consider it belonged to the genus *Leda*, in other words to the Nuculanacea of today's classification. But he was not able to see the hinge which, as described here, clearly excludes *Thoralia* from that superfamily. The new family is created here because the particular combination of nuculoid shape and subumbonal cardinal teeth has not previously been encountered.

Thoral compared *T. languedociana* with two species described by Barrande (1881) from the Ordovician of Bohemia which he also placed in '*Leda*'. One of these was *Leda bohemica* Barrande (1881 : pl. 269), but it is an entirely different shape, with posteriorly-placed umbones and the posterior part of the shell taller than the anterior part. It also has taxodont hinge teeth, and so belongs to the family Praenuculidae and possibly the genus *Praeleda*. The other was *Leda incola* Barrande (1881 : pl. 270, fig. 111), which is a more elongate species which Barrande showed to have fine-scale taxodont teeth on a long narrow hinge plate posterior to the umbones. This is apparently an early species of the Malletiidae. Neither species has characters suggesting any close relationship with *T. languedociana*.

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